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The Basking Shark

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Introduction

The basking shark (*Cetorhinus maximus* Gunnerus) is the second largest fish species known to man and is exceeded in size only by the whale shark from the Pacific, yet it has attracted only a small scientific literature and a few popular accounts of its associated fisheries. The reasons for this revolve around the difficulties and costs involved in studying such large animals at sea, compounded by the fact that for the greater part of the year their whereabouts are unknown. The species has been exploited by man for several centuries and today forms the basis of fisheries both in the north-east Atlantic and around Japan in the Pacific.

Taxonomy

The relationship between basking sharks and other species of cartilaginous fish is shown in Figure 1, following the classification of Compagno (1973). The classification of elasmobranchs is not without controversy, and the figure is merely intended to indicate the affinities of basking sharks with other forms. Synonyms for the species name are to be found in early accounts of basking shark biology and include among others *Selachus maximus* (Minding), *Squalus maximus* (Gunnerus) and *Selache maxima* (Cuvier). The genus *Cetorhinus* is thought to be distinct within the lamniform sharks and it is included in a family of its own, although some earlier classifications include it with the Lamnidae in a combined family, the Isuridae. Maisey (1985) suggests that the recently discovered megamouth shark, *Megachasma pelagios* Taylor, Compagno & Struhsaker, should also be included in the Cetorhinidae and not in a separate family as suggested by Taylor, Compagno & Struhsaker (1983).

Although uncertain, it is probable that there is only a single species of basking shark (Matthews, 1962), despite suggestions of other species within the genus. Springer & Gilbert (1976) discuss the proposition that there are at least four species, two in the north Atlantic/Mediterranean and one each from the south Atlantic and waters around Australia. Separation into species is based mainly on differences in body proportions. Such differences occur naturally during growth, and Springer & Gilbert therefore argue that the specimens on which the division into species is based merely reflect these changes. They conclude that there are insufficient reasons for separation.

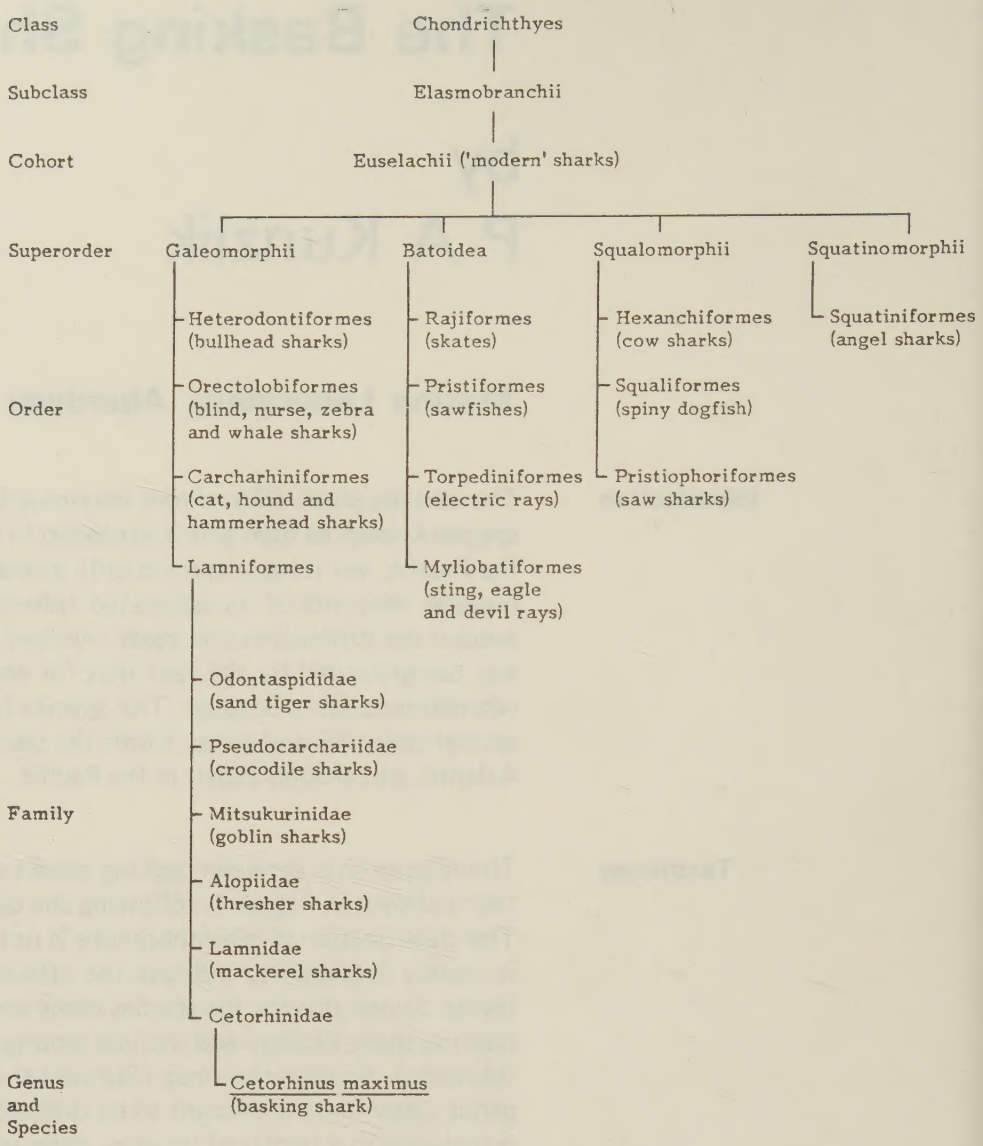

Figure 1. **Interrelationships of living elasmobranchs according to the classification of Compagno (1973). Filter-feeding is seen in basking sharks (Lamniformes), whale sharks (Orectolobiformes) and mobulid rays (Myliobatiformes) and is a habit thought to have evolved independently in each group (Moss, 1977). It is interesting to note the relationship between the basking shark, a harmless planktonivore, and the Lamnidae containing such a renowned "man-eater" as the great white shark.**

Distribution

Knowledge of the distribution of basking sharks is based on recorded sightings of the species in the surface layer of continental shelf waters, from stranded individuals or from incidental capture below the surface. On the whole these sightings refer to observations made during late spring and early summer, and consequently the winter distribution of basking sharks is not known for other than presumed strays. One exception concerns the appearances of basking sharks around Monterey Bay, California, which are reported to be most numerous during the winter months (Squire, 1967).

Bigelow, Farfante & Schroeder (1948) describe basking sharks as inhabitants of temperate and boreal waters, their northern limits in the Atlantic following the transition zone between Atlantic and Arctic waters. In support of this they are seen as far north as the Gulf of Maine, to the south and west of Iceland and off the North Cape of Norway. They are also seen regularly,

but infrequently, east of the North Cape in the Russian White Sea (Konstantinov & Nizovtsev, 1979). The southernmost limits of sightings within the north Atlantic lie off Florida in the west (Wood, 1957) and Senegal in the east (Springer & Gilbert, 1976). From the north Atlantic they extend eastwards into the Mediterranean, and in the south Atlantic they have been observed in both South African and Argentinian waters. In the Pacific they are present off the coast from California to British Columbia, though less common off Oregon and Washington (Squire, 1967), and are also present around Japan and off the Chinese coast. They are seen in the south Pacific off Peru, Equador, southern Australia and New Zealand.

Observations of basking sharks are notably absent from tropical regions of both the Atlantic and Pacific oceans, yet despite this their appearance in both northern and southern latitudes is taken to indicate some trans-equatorial movement (Briggs, 1960). This idea is given credence by the fact that submergence in deeper waters beneath the thermocline, as witnessed by long line catches, is not unknown in the tropics for some large, temperate sharks. Unfortunately, as it is unlikely that basking sharks would be caught in this way their absence from such catches can neither confirm nor deny their presence in deeper tropical waters (Springer & Gilbert, 1976).

Morphology and Structure

Much of what is known of the morphology and structure of basking sharks comes from the publications of Bigelow *et al.* (1948) and Matthews & Parker (1950). An abbreviated summary of their descriptions is given here with additional references cited where necessary.

There is some confusion over the actual coloration of basking sharks owing, in part, to observations based on sharks removed from the water. In addition, as the skin is highly textured its appearance varies greatly under different lighting conditions. As a consequence Maxwell (1952) disputes the description of a dark grey, almost black coloration with varying amounts of light grey or white along the undersurface, claiming that the scientific accounts have a tendency to exaggerate the darkness of the body. Another former fisherman describes the sharks as brightish in water, with python-like markings on the back, but dull grey out of water, with the back markings only faintly visible, and a dull white belly (Watkins, 1958).

For the largest specimens the first dorsal fin has a height approaching 2 metres (m), approximately the same length as each of the pectoral fins and also roughly the distance which separates the tips of the upper and lower lobes of the tail fin (see Fig. 2). The combination of a crescent-shaped tail, long gill openings, long rakers on the gill arches, a multitude of disproportionately small teeth and nostrils which are widely separated from the mouth serves to separate the basking shark from other shark species. As with all sharks the males of the species are recognised by a pair of claspers (copulatory organs) extending from the base of the pelvic fins. In both sexes the body is described as fusiform (cigar shaped) and reaches lengths in excess of 10 m, although considerable doubt surrounds the maximum length attained. Parker & Stott (1965) quote a theoretical maximum length of 12.26 m, later corrected to 12.76 m. Holden (1974) records a maximum size of 13.72 m, but this measurement is of uncertain reliability. The snout of larger specimens is very short and almost conical with a rounded tip, although in younger individuals it forms an almost cylindrical proboscis, the transition between juvenile and adult forms occurring most commonly at lengths between 3.5 m and 5 m. It has been suggested that the description of the juvenile form is due to differential shrinkage of tissues in the specimens observed. However, Springer & Gilbert (1976) describe a proportionately longer snout as undoubtedly a juvenile condition.

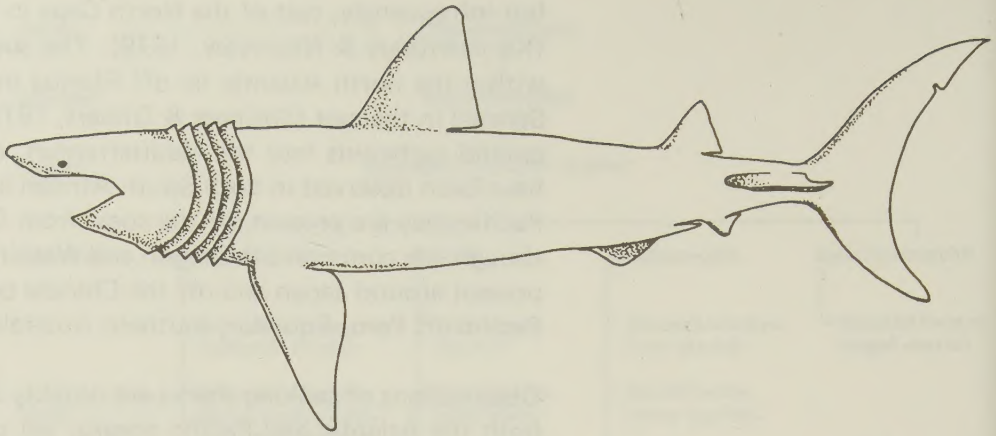

Figure 2. **Line drawing of an adult basking shark (7.5 m) based upon measurements of 10 individuals. (Redrawn from Matthews & Parker (1950) with permission).**

There are five enormous pairs of gill arches which extend from the upper sides to the lower surface of the throat. The first pair are the largest and almost join on the underside, subsequent pairs becoming smaller and the distance between their lower margins increasing. The gill arches support two distinct structures, with oxygen exchange between sea water and the shark's blood taking place across the highly vascular gill lamellae after the water has been filtered by a series of stiff but flexible gill rakers. The rakers are deciduous, being shed in north-east Atlantic specimens during October and November and not being replaced until the following February (Parker & Boeseman, 1954). Individual rakers may reach 0.15 m in length and they number 1,000 to 1,300 rakers per arch.

The skin is covered by numerous small, thorn-like denticles which are fairly evenly distributed over the body and which point unidirectionally towards the tail, making the skin feel relatively smooth if stroked the "right" way and exceedingly rough if stroked towards the head. Springer & Gilbert, (1976) described an individual shark on which the denticles pointed in all directions, although there was some evidence to suggest that their specimen was not in prime condition. Almost bare furrows run along lines of apparent flexure of the skin, which is evenly covered by a layer of mucus below the height of the denticles, although they too become covered by a layer of slime after death as mucus extrudes from glands in the skin, especially if the shark is removed from the water. Lesions, associated with breeding activities, are often apparent in the region of the cloaca. The teeth are modified denticles and the mouth contains four to seven functional rows on each jaw with or without other non-functional rows, that is, rows not rigidly joined to the jaw. On either side of the jaw each row may contain upwards of 100 teeth reaching a height of five to six millimetres in larger individuals.

Although the skeleton of sharks may be more or less calcified it is, nevertheless, formed from cartilage and not bone. Whereas most species of fish can be satisfactorily aged from annual growth "rings" on scales or bony structures, sharks cannot. Within the centra of the vertebrae of sharks there exist alternate dark and light concentric rings with some degree of calcification actively proceeding in the light, outermost, most recently formed rings. These rings have been shown to form annually in some species of shark, for example, the blue shark (Stevens, 1975) and the leopard shark (Smith, 1984) although their rate of formation in basking sharks remains uncertain. On the

basis of indirect evidence Parker & Stott (1965) concluded that seven calcified rings are present at birth and that subsequently two rings are formed each year. This may not be a constant feature as the number of rings per centrum diminishes towards the tail according to Parker & Stott (1965), and this differential rate of ring formation is explained in terms of a structural response to varying degrees of stress along the length of the shark. As yet no direct evidence of the rate of ring formation exists.

The liver has two main lobes running the length of the abdominal cavity and is moulded to the shape of the cavity walls and organs. It may account for up to 25% of the weight of an individual shark, although McNally (1976) records a more general figure of one sixth body weight, yielding up to 75% liver oil. The oil contains a high proportion of squalene, a terpenoid hydrocarbon used in the cosmetic and aviation industries, which accounts for much of the commercial value of the fish. Marine Laboratory records from the early post-war Scottish fisheries show the oil to contain 38% squalene, although a lower value of 33.6% is recorded for Californian basking sharks (Kayama, Tsuchiya & Nevenzel, 1969).

It is likely that the liver acts as a hydrostatic organ, increasing the buoyancy of the shark and reducing the dependence on hydrodynamic lift given by the pectoral fins and undersurface of the shark when in motion, yet despite this the basking shark remains negatively buoyant and will sink when dead. Springer & Gilbert (1976) observed a stray basking shark in the Gulf of Mexico with 63.8% squalene in the liver oil and suggest that such a disproportionate increase of this low density hydrocarbon in shark livers would lead to increased buoyancy and a loss in swimming control, resulting in strays and strandings. It is also possible that the liver acts as a food store to maintain the animals over winter. However, indications are that in large sharks control of buoyancy takes priority over food reserve as a function of the liver oil (Baldridge, 1972).

Feeding

Basking sharks feed by swimming open-mouthed (Fig. 3) with their gill rakers erect and extended across the gaps between gill arches, thus forming a sieve which filters particulate matter of a suitable size from the respiratory stream of sea water. When the mouth closes the rakers collapse and are assumed to deposit the filterable matter onto a mass of mucus, produced by glands at the base of the rakers, which is then swallowed. The stomach contents form a characteristically red, semi-liquid "soup", which has been estimated to weigh over 0.5 tonnes (t) in an average shark but contains less than 30% organic matter, much of which is mucus (Matthews & Parker, 1950). Recognisable food items in the stomach include copepods, arrow-worms, larval crustacea and fish eggs (Matthews & Parker, 1950; Parker & Boesman, 1954). Mutoh & Omori (1978) examined the gut contents of a basking shark caught off Japan and concluded that it had been feeding at night on oceanic shrimps at a depth below 100 m.

The maximum filtering rate of a 7 m shark has been calculated as 1484 m^3 of water per hour assuming a mouth area of 0.4 m^2 (0.72 m gape) and a swimming speed of 2 knots (Parker & Boeseman, 1954). In the process approximately 212 kilocalories per hour are thought to be expended, a level at which a net energy loss would occur if feeding continued throughout winter, at least in the north-east Atlantic. This, in association with the autumnal loss of rakers and the winter absence from coastal areas, suggests a resting, non-feeding period in winter accompanied by a cessation of growth (Parker & Boeseman, 1954).

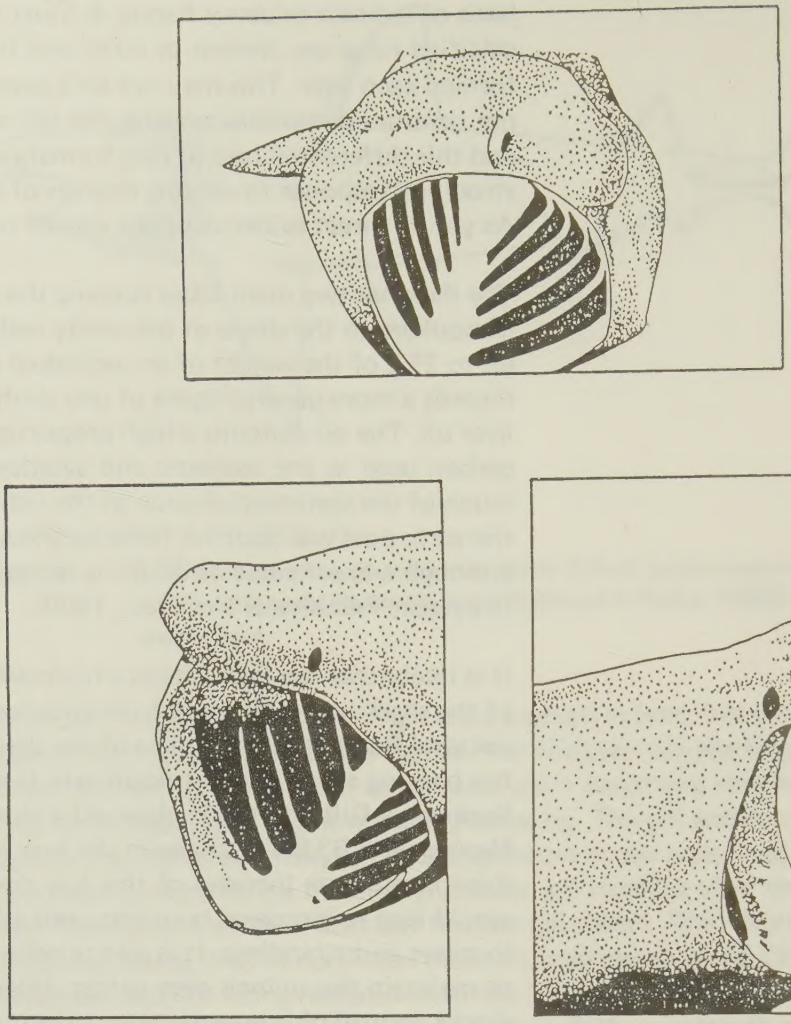

Figure 3. **Appearance of the snout and mouth of a basking shark while feeding, showing clearly the gill arches through which sea water passes. The original photographs from which these drawings are taken were of a shark with a mouth width of 1 m. (Redrawn from Hallacher (1977) with permission).**

Reproduction and Growth

From an examination of their internal anatomy Matthews (1950) assumed ovoviviparity in basking sharks, that is, live young are produced from eggs which hatch within the body. This is not unusual in elasmobranch fish. However, the basking shark appears to be unlike any other elasmobranch in that it possesses a single functional ovary, the right one, containing a very large number of small eggs rather than the smaller number of larger, heavily yolked eggs more commonly found. Fertilisation is internal; the male's claspers are inserted one by one into the female's cloaca and sperm-filled vesicles (spermatophores) are transferred from the male to the female. It is thought that pairing takes place in the early summer as all the females examined by Matthews (1950) during late May showed signs of recent copulation, freshly healed or open wounds caused by the male's claspers. One female contained spermatophores. It is not known whether female basking sharks share the characteristic of many other shark species, for example the blue shark, in which females are able to store sperm for many months before fertilisation of their eggs. The period of gestation is not known, although Parker & Stott (1965) suggest a period of 3.5 years based upon their postulated age-length relationship for this species. However, length-frequency analysis of their data suggests a period of just over one year (Holden, 1974) and represents a more probable value according to Stott (1984).

The assumption of ovoviviparity is supported by the report by Sund (1943) of a Norwegian fisherman catching a female specimen which proceeded to give birth to five live young and one still-born, estimated to be between 1.5 m and 2 m long. Although records rarely show individuals less than 2 m long Parker & Stott (1965) record the two smallest observed specimens as measuring 1.68 m and 1.8 m in length and it seems probable that length at birth lies between 1.5 m and 2 m. There is no reason to believe that the sex ratio of the young produced is not 1:1. The catch from commercial fisheries is predominantly of females, yet despite this no reliable observation has been made of a pregnant basking shark other than the Norwegian example quoted above. Because of this Matthews (1950) assumed some movement away from the summer grounds of pregnant females after copulation or the adoption of some habit preventing their capture; for example, they may swim at greater depths. Also because of this it is assumed that females give birth to their young during their seasonal absence, possibly immediately prior to their coastal appearance, which would give the young a full season to feed and grow before overwintering. The Norwegian observation of a captured female giving birth to live young, however, took place in August, towards the end of their seasonal presence in those waters.

As it is not easy to age individuals, most attempts to describe the growth of basking sharks have been based on length-frequency analysis whereby successive modes in the length-frequency distribution are attributed to successive age groups. Growth curves from three such analyses are shown in Figure 4; the solid line (Matthews, 1950) and the dashed line (Parker & Boesman, 1954) show few differences despite a three-fold increase in observations. However, a further 50% increase in sample size alters the curve markedly as shown by the dotted line from Parker & Stott (1965). The fact that the curve changes so markedly simply by the addition of a relatively small number of measurements highlights the problems caused by such small sample sizes in these length-frequency analyses. Furthermore, this method is thought to be of little use for shark species owing to their relatively slow rates of growth (Holden, 1974). The allocation of age to any given length must, therefore, be considered uncertain. It is, therefore, particularly difficult to assess the age at which basking sharks become sexually mature. The length at which females mature is not known; for males it has been estimated to lie between 4.6 m and 6.1 m on the rather limited evidence that only small claspers are found on male basking sharks less than 3.4 m long and very large claspers are found on males greater than 7.6 m in length (Bigelow *et al.,* 1948). Matthews (1950) examined a male which was just approaching sexual maturity at 6.9 m, a length which does not seriously contradict these limits.

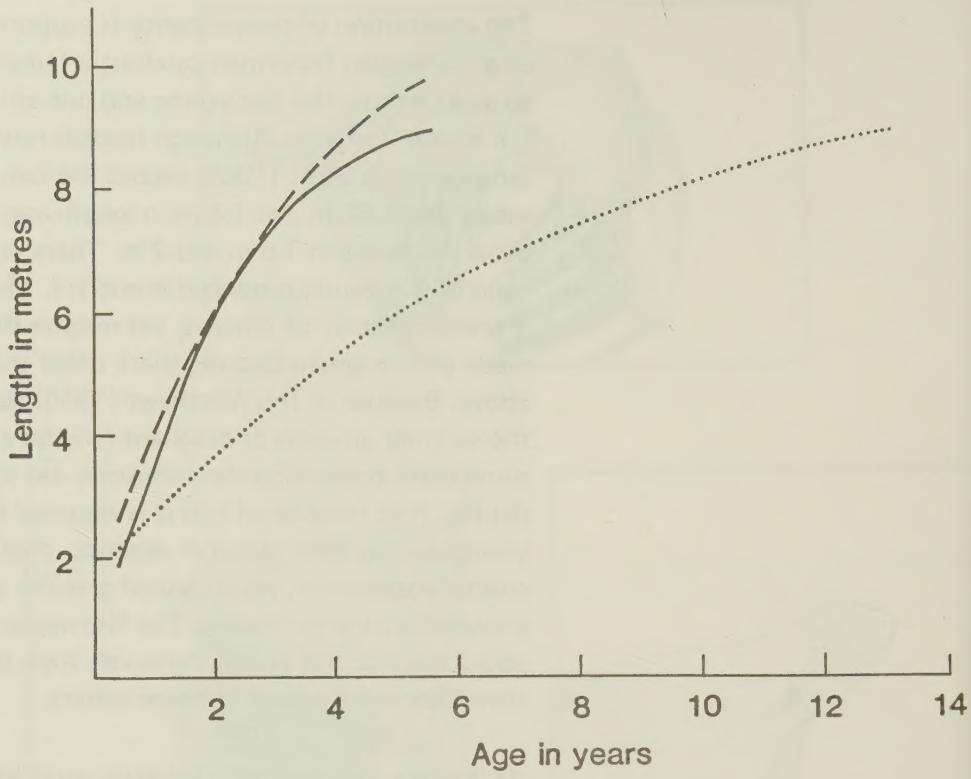

Figure 4. **Three postulated growth curves based on length-frequency analyses of stranded and captured basking sharks. The solid line is a curve based on 19 measured specimens (Matthews, 1950), the dashed line is one based on 60 measurements including most of the previous 19 (Parker & Boeseman, 1954) and the dotted line is one based on 93 measurements including all the previous 60 (Parker & Stott, 1965). (Owing to differences in the dimensions measured (Parker & Boeseman, 1954) the lengths represented by Matthews' curve should be increased by a factor of 1.11 for strict comparability).**

Behaviour and Migrations

Basking sharks are most often seen during late spring and early summer on clear, sunny days swimming singly, in pairs or in larger groups close to the surface and with their dorsal fin clear of the water. The upper lobe of their tail fin may also break the surface as, exceptionally, may the tip of the snout. It is this basking habit which gives the sharks their name. They undoubtedly feed when close to the surface, and Priede (1984) observed them traversing plankton patches and altering course to remain within the patch. However, it is not known why they favour the surface when greater plankton concentrations may be found deeper in the water column, a feature observed by Maxwell (1952). Feeding sharks have been observed to close their mouths at intervals of between 30 and 60 seconds and periodically to expel excess water through the gill slits prior to swallowing their food (Hallacher, 1977). Basking sharks sometimes breach, the shark leaping from the water and falling back again with a resounding crash. So improbable was this action considered by Matthews & Parker (1950) that they suggested such observations confused basking sharks with dolphins or thresher sharks, their comments were later withdrawn unreservedly after correspondence with basking shark fishermen (Matthews & Parker, 1951).

Matthews (1950) related the basking habit to the breeding behaviour of the sharks. However, his observations were incomplete and this explanation was subsequently rejected by both Maxwell (1952) and Watkins (1958) on the grounds that many immature sharks also bask among the adults. Despite this

there is evidence to suggest that it is mainly the females which adopt the basking habit; commercial catches taken at the surface indicate an average sex ratio of 18 females to every male (Watkins, 1958), rather less than the 30 to 40 females per male quoted by Matthews (1950), whose figure originated from Watkins and was based on the catch from only a single season. In the current Scottish fishery, whenever large numbers are observed the sex ratio is reported to be never less than 10 females per male. This is not, however, reflected in the overall catch, from which a smaller ratio is recorded, probably owing to the catching of isolated males which are said to be sometimes found at the surface when conditions do not suit the normal basking habit. Inadvertent sub-surface catches from around Newfoundland give a sex ratio of just over two males per female (Lien & Fawcett, 1986), and it is possible that in the normal course of events male basking sharks swim deeper than females and are simply not as evident at the surface. Although very large shoals of more than 100 basking sharks have been seen these are generally observed further offshore; Watkins (1958) records the average shoal in the Clyde sea area as comprising three or four sharks.

Two hypotheses have been proposed regarding the seasonal movements of basking sharks, based on observations made within the north-east Atlantic. Historically it was thought that they overwintered off the Moroccan coast, migrating northwards in the spring, and that this explained their appearance firstly off the coast of Portugal and then with sightings progressing chronologically northwards up the western coasts of Europe, that is, off the headlands of south-west England, then Ireland and the Isle of Man, around the Western Isles of Scotland and, finally, off the coast of northern Norway. This suggests a single parent population from which all observations and commercial catches from western Europe were taken. This chronology has often been disputed and Bigelow *et al.* (1948) stated that a lack of evidence for any southward increase in abundance during autumn and winter suggests that they simply disperse offshore and overwinter in deeper waters, lying inactive on or close to the bottom. As squalene is found in large quantities only in the livers of deep-water sharks (Baldridge, 1972), the presence of an intermediate level as found in basking sharks provides circumstantial evidence for the adoption of at least a moderately deep water habit for a part of their life-history. Matthews & Parker (1950) even doubted whether a northwards succession of appearances occurs irrespective of cause, stating that basking sharks appear on all western European coasts at or about the same time. It is generally assumed that the return of the sharks to coastal waters during spring is associated with periods of high biological production when supplies of their planktonic prey are plentiful. Priede (1984) speculated that the feeding behaviour of basking sharks is likely to be related to frontal regions between different water masses where planktonic production is high. It also appears that temperature may influence their distribution. In discussing incidental captures off the coast of Newfoundland, Lien & Fawcett (1986) found that captures rarely occurred until water temperatures reached 6°C and were not common until a temperature of 8°C was reached; 90% of captures were made at temperatures between 8°C and 12°C. Although these water temperatures may merely correlate with the normal seasonal appearance of basking sharks, and not be the cause of it, it is interesting to note that at Monterey Bay, California, where they are most abundant during winter, they are least abundant when water temperatures are close to or greater than 14°C (Squire, 1967) and that the presumed stray examined by Springer & Gilbert (1976) although found in water of 20°C was apparently a sickly specimen and very close to death. It is possible that such temperature effects explain the absence of basking sharks from tropical surface waters.

In addition to their seasonal presence there is also an apparently cyclical nature to the abundance of basking sharks. Bigelow *et al.* (1948) concluded that published records demonstrate much variation in basking shark abundance over periods of years, citing their scarcity off the Norwegian coast during the first half of the 18th century and the middle of the 19th century which alternated with periods of abundance around 1800 and 1880. There was also a dearth of basking sharks off the west coast of Ireland during the 1830s according to McNally (1976), who also reports that in the early years of this century they were observed off County Waterford, Ireland, having not previously been recorded there, and also that during the 1930s they became more numerous in British waters. This last point supports the observations of Dr A. Vedel Tåning of the Danish Fisheries Research Institute, Charlottenlund, who in correspondence with the Marine Laboratory wrote in 1948 of an "interesting increase" in basking shark numbers from Iceland to Morocco, its occurrence having been recorded several times during the period 1928–48 from Danish waters where no previous record existed for at least 100 years. Furthermore, recent observations (Kenney, Owen & Winn, 1985) showed basking sharks to be currently more common off the mid-USA Atlantic coast than indicated by Bigelow *et al.* (1948).

Basking Shark Fisheries

Several nations have exploited basking sharks at the time of their seasonal inshore movements, the history of some fisheries extending back hundreds of years. Until this century such fisheries formed the basis of cottage industries, supplying oil for lighting and tanning and occasionally food and shark skin leather, generally depending on the use of hand harpoons launched from small boats to catch their quarry. As the first reaction of a harpooned basking shark is to sound rapidly, the ensuing struggle to bring it to the surface was often perilous. During this century, manual harpooning has gradually given way to the use of non-explosive harpoons fired from small whale guns and in one case the use of nets. Several fisheries developed around the time of World War II in response to the general shortage of commodities, and relied on markets for liver oil products which later declined in response to increased supplies of mineral oils and the advent of synthetic vitamin production. Some of these fisheries are discussed below.

California

Between 1924 and 1937 a small enterprise was established off the Californian coast catching basking sharks for reduction to fishmeal and for the sale of shark liver oil as a "cure-all" tonic (McCormick, Allen & Young, 1964) (in Japan squalene is still sold as a panacea for all ills (Clark, 1981)). Shortly after the war a large scale basking shark fishery was established by a group of fishermen using equipment surplus to the requirements of the United States armed forces. An aircraft was used to spot basking sharks at sea and to direct the crew of an amphibious vehicle towards them until a suitable shark could be harpooned from the front of the vehicle and shot with a rifle when, or if, the catchers could return it to the surface. Off Monterey Bay, California, up to 200 basking sharks were taken annually in this way from 1946 to 1949 (Roedel & Ripley, 1950) until the price of livers dropped and made the operation uneconomic. Vitamin extraction and fishmeal production provided the main markets for this fishery, although olive oil racketeers often bought squalene with which to adulterate cheap blends of cooking oil (McCormick *et al.* 1964).

Norway

Norwegian fishermen have long been the major catchers of basking sharks in the north-east Atlantic. Their fleet has prosecuted local Norwegian fisheries from the Barents Sea to the Kattegat as well as more distant fisheries ranging across the North Sea and as far as to the south and west of Ireland and to Iceland and Faeroe. Their fisheries generally start around April and May, although perhaps as early as March in some years, reach their peak in June

and finish in August or, less commonly, September, after which the fleet diverts either to trawl for shrimps or to assist vessels in other fisheries (Myklevoll, 1968). The fleet itself comprises small wooden vessels 15 m to 25 m in length which are sometimes used for hunting small whales as well as basking sharks (Plate I). The shark harpoons, fired from a small whale gun mounted on the bow, differ from those used in whaling (Myklevoll, 1968); non-explosive harpoons are used because explosive devices damage the shark to the extent that the harpoon dislodges easily and the fish is lost. Although in times of hardship the flesh has been used for food, only the livers are normally utilised and are extracted from the shark while still at sea where the carcass is dumped. The fins may also be retained if a pre-arranged market for them exists. The number of boats taking part in the fishery varies from year to year and depends on the volume of liver oil which the market will absorb and the price offered. Both these factors are determined during pre-season discussions between the fishermen and processors and result in quotas for each boat which are based upon the overall quantity of livers for which sales are agreed and the number of boats electing to fish for basking sharks (Anonymous, 1968; Stott, 1982). The demand and price paid for basking shark livers is now much reduced as supplies of squalene-rich liver oil from the gulper shark, *Centrophorus granulosus* (Block & Schneider) have recently undercut the Norwegian market (S. Myklevoll, personal communication).

Plate I. **A Norwegian basking shark vessel. Built in 1957, the "Feiebuen" is typical of the ageing fleet of Norwegian catchers. The harpoon gun can be seen mounted in the bows and the net for lifting aboard the liver is visible over the hold. An elevated walkway running from the wheelhouse to the bows allows the marksman easy access to the gun after the lookout, visible in the crow's next, has located their quarry.**

The geographical and temporal distribution of the domestic Norwegian fishery, which changes markedly from year to year, was discussed by Stott (1982), who suggested that survival of both fish and fishery is due to the unpredictable nature of the sharks' inshore migration. Norwegian landings

are initially recorded as liver weight. Total Norwegian catches in numbers from 1946 to the present are given in Table I, assuming a mean liver weight of 0.5 t. Norwegian fishermen are known to have been actively fishing for porbeagle sharks off the Scottish coast as early as 1934, and although it is not known when they first started fishing there for basking sharks, their Scottish fishery was certainly being prosecuted in the immediate post-war years after the establishment of several native Scottish fisheries. After the establishment of the post-war Irish fisheries, Norwegian fisherman also became active in Irish waters. The sizes of the early Norwegian catches from waters off Scotland and Ireland are not known. UK and Irish membership of the European Community (EC) and the extension of fishery limits have recently formalised Norwegian fisheries in these waters. Agreement was reached in 1978 on catch regulations between Norway and the EC following the imposition of 200 miles fishery limits in the 1970s. The Norwegian catch of basking sharks in EC waters has since been limited by quota and currently stands at 400 t liver weight annually. Actual catches are much less than this. In UK waters, Norwegian vessels may not fish for basking sharks or other species within the 12 miles belt. The Norwegian basking shark fleet is an ageing one, and as the boats reach the end of their useful working life they are being withdrawn from the fishery with no sign of replacement. Since 1983 twelve Norwegian basking shark boats in transit to the Irish fishing grounds have been repeatedly observed in Scottish waters by fishery protection vessels. By 1987 only seven of the twelve remained on the registry of Norwegian fishing boats. Such a diminution is due in part to restrictions on their whaling activities. However, the fishery has always been an uncertain one and the problems encountered in catching and marketing basking sharks and their products have not encouraged younger fishermen to enter the fishery (S. Myklevoll, personal communication).

Ireland

In 1947 a fishery using specially constructed nets to capture basking sharks was established on the west coast of Ireland at Keem Bay, Achill Island. Nets and harpoons were used in the developmental years of the fishery, but by 1951 nets alone were used either to actively encircle a previously spotted shark or to entangle sharks in set nets as they swam around the margins of the bay (McNally, 1976). When set, the net was firmly attached to the shore by a hawser and formed a vertical sheet extending for three-quarters of its length in a line perpendicular to the edge of the bay. The last quarter was almost doubled back on itself and held in place by anchored floats. This configuration allowed the net to collapse in on the shark when hit, yet remain firmly coupled to the shore (McNally, 1976). The sharks caught in the nets were killed by lancing through the spinal cord. Initially only the liver oil was of value from this fishery, but in later years both the flesh and fins were marketed for human consumption. The numbers taken annually in the Achill Island fishery over the period 1947–75 are given in Table I, from which it is seen that the catch declined from a peak of 1,808 in 1952 to 38 in 1975. Parker & Stott (1965) modified the hypothesis of inshore and offshore migrations (Bigelow *et al.*, 1948) to include the concept of local, discrete stocks in order to explain the decline in catch, attributing it to overfishing of a local stock.

After the re-introduction of harpoons to the Irish west coast fishery in 1973, the following two years saw 17 and 36 sharks respectively caught in addition to those netted; these years also saw the establishment of an Irish harpoon fishery off the south-east coast of Ireland which contributed to a catch of 180 and 350 sharks (McNally, 1976).

Table I

Commercial basking shark catches (numbers) 1946–86

Year	Scotland	Ireland (Achill)	Norway*	Year	Scotland	Ireland (Achill)	Norway*
1946	66**		426	1967		41	4,180
1947	245**	6	250	1968		75	3,160
1948	222**	80	964	1969		113	3,130
1949	35	450	782	1970		42	3,774
1950	77	905	1,764	1971		29	1,708
1951	147	1,630	806	1972		62	1,438
1952	68	1,808	392	1973		85	2,214
1953	110	1,068	596	1974		33	2,148
1954		1,162	682	1975		38	3,670
1955		1,708	294	1976			1,502
1956		977	528	1977			1,586
1957		468	258	1978			1,570
1958		500	122	1979			2,268
1959		280	2,532	1980			1,606
1960		219	4,266	1981			776
1961		258	2,042	1982			930
1962		116	1,266	1983			758
1963		75	2,210	1984			888
1964		39	2,138	1985			631
1965		47	1,304	1986			493***
1966		46	1,822				

* Assumes a mean liver weight of 0.5 t.

** Minimum value. Up to 300 taken annually during 1947 and 1948.

*** Provisional value.

Data sources: Department of Agriculture and Fisheries for Scotland (DAFS), Marine Laboratory, Aberdeen; McNally (1976); Norges Fiskeristatistikk; Norges Fiskeridirektoratet; Norges Fiskerier. Current Scottish catches are attributable to only a single fishing vessel and for reasons of confidentiality DAFS are not at liberty to disclose them.

Scotland

Several attempts were made to establish United Kingdom fisheries off the west coast of Scotland during the years before and after the war, most notably but probably least successfully by the author Gavin Maxwell. All of these proved to be short lived owing to economic failings and marketing difficulties, and the several books produced to chronicle their histories (Maxwell, 1952; O'Connor, 1953 and Watkins, 1958) may well have proved more remunerative than the fisheries themselves. The method of capture varied from hand harpooning from small catcher boats working with a larger mother ship to the use of Norwegian small whale guns mounted on former herring ring-netters working to a shore based factory or a factory ship. Experiments with nets were conducted, but this mode of capture was not implemented in Scottish waters. The Clyde and the Minch were the main hunting grounds, with the season extending from May to September in the Clyde, but with numbers decreasing from mid-June onwards elsewhere, although large numbers were occasionally seen as late as October in the Minch (Watkins, 1958). No more than 300 sharks were taken by UK fishermen in any one year and their catches are given in Table I. To reflect the true numbers taken off the Scottish west coast at that time an unknown proportion of the Norwegian catch must, of course, be added to these figures. Other than marketing problems the main difficulty faced by the Scottish

fishermen was the erratic nature of the movements of basking sharks into west coast waters. Watkins (1958) described the Clyde as a particularly erratic fishing ground for basking sharks, adding that in some years the sharks are almost a plague yet in other years they are very few. These observations fit in with records of the Marine Laboratory, Aberdeen, including those taken from observations by fishery protection vessels (1953–59), which indicate that the summer distribution of basking sharks extends along the entire west coast of Scotland, with most sightings recorded from the Minch and Clyde, suggesting that these are major centres of summer concentration. From these observations Rae (1956) concluded that the summer movement onto west coast grounds varies considerably from year to year, with the heaviest concentrations found in the Minch and large numbers only occasionally entering the Clyde. The unpredictable nature of basking shark abundance and distribution off the Scottish west coast is outlined in Table II, from which no discernible pattern is evident. A year of high abundance may be followed by one of scarcity and *vice versa;* the invasions may spread along all or part of the west coast or be virtually non-existent; movements into areas not normally associated with the local geographical distribution of basking sharks are apparent and so are their unseasonal appearances in some years.

Table II

Relative abundance of basking sharks off the Scottish coast

1935	Unusually large numbers in the Minch.
1937	Unusually prolific, heavy invasion of the Clyde.
1947	Large numbers off Cromarty during October and November, a very unusual occurrence.
1949	Large numbers in the Clyde.
1953*	Excessive numbers; widespread from the Clyde to north of Cape Wrath. The outstanding year along the west coast during the 1950s (and up to 1964, at least in the Clyde).
1954*	Not exceptional.
1955*	Considerably less than 1953; present from the Clyde to the Butt of Lewis.
1956*	Considerably less than 1953; almost none south of the latitude of Stornoway.
1957*	Not exceptional.
1958*	Numerous in the Clyde, scarcer than usual along the rest of the west coast.
1959*	Scarcest on the entire west coast since fishery protection vessel records began.
1961	Surprising numbers off the east coast, not exceptional on the west coast.
1962	Even greater numbers on east coast grounds than in 1961 and mainly during the period January to April.
1963	Scarcer on the west coast than for some years.
1964	Heavy invasion into the Clyde and off the Wigtownshire coast, possibly the most in the Clyde since the war.

* Fishery protection vessel records

It is rather ironic that the squalene content of the liver oil which, in part, formerly made basking shark livers unmarketable as far as UK fishermen were concerned and which contributed to the downfall of their fisheries, is now one of the attributes that makes the liver attractive to buyers and which has contributed to the re-establishment of a fishery in the Clyde. Along with industrial sales of liver oil, the fins, for shark-fin soup, and flesh are sold for human consumption and, latterly, some interest has been shown in utilising the cartilaginous skeleton. (Recent work has shown the cartilage of basking sharks to contain a substance which restricts tumour growth (Lee & Langer, 1983)). The modern fishery was established in 1983 and is prosecuted within the Clyde sea area and the Irish Sea (as far south as the Eire – Northern Ireland border) by a single boat rigged for light trawling which diverts to basking sharks when they are available, harpooning them from a gun mounted in the bows. This contrasts with the earlier post-war Scottish fisheries which were wholly reliant on shark fishing during the summer months.

The vulnerability of sharks to fishing is not only dependent on their presence, bearing in mind the unpredictable nature of their invasions, but also heavily dependent on fine weather, which may bring the sharks to the surface and allow them to be seen. This dependence, which applies to all harpoon basking shark fisheries, was noted in other circumstances by Priede (1984), who tracked a marked basking shark in the Clyde for 17 days during which time it remained on the surface for one day only, the only sunny day in that period. Otherwise it surfaced only intermittently. Because of these constraints fishing is necessarily opportunistic, with effort varying considerably within a season and also from year to year.

Stock Structures

The concept of a series of localised and discrete stocks (Parker & Stott, 1965) has recently been applied to basking sharks in attempts to evaluate the threat posed by commercial fishermen, for example, in the modern Clyde fishery (Horsman, 1986). It is worth evaluating this concept in the light of available evidence. Priede (1984) tentatively proposed a resident summer population of basking sharks in the Clyde on the basis of satellite tracking of a marked individual, but as has been seen already the variable nature of movements into the Clyde appears to exclude this possibility and the strong annual variation in numbers described in Table II points towards the animals forming only part of a larger stock, a varying proportion of which may be found in the Clyde each summer. While it is possible that those entering the Clyde in early summer remain resident for the whole season it is unlikely they form a distinct stock. Do they then form part of a single stock to the west of Scotland or are they drawn from a wider area, for example, to the west of the British Isles or even the whole of the north-east Atlantic?

Acceptance of the hypothesis that the Irish fishery collapsed owing to over-fishing of a local stock would seem to preclude the concept of a larger stock to the west of Britain and Ireland. However such acceptance implies a stock of basking sharks so discrete, local and loyal to a small summer feeding ground that it could be almost eliminated by static gear exploitation in a single bay. Parker & Stott (1965) sought to explain the decline in catch at Achill by postulating the existence of such a stock, which was believed to have diminished in size as a direct result of exploitation. Although in its simplicity this is an attractive hypothesis, it fails to take into account other features of the fishery affecting the catches. For example, fishing effort is likely to have diminished, in part because two of the three registered companies that prosecuted the fishery were wound up as unprofitable and several independent groups also withdrew (Went & Suilleabhain, 1967; McNally, 1976). It does seem that the sharks made fewer incursions into the

bay, but in view of the unpredictable nature of invasions to the Scottish and Norwegian coasts this would not be entirely unexpected, even more so as both Went & Suilleabhain (1967) and McNally (1976) documented earlier unpredictable inshore movements for the Irish coast. (It is clear that fluctuations in numbers invading from year to year were a crucial factor in the development of 19th century Irish fisheries, deterring investment in the industry owing to the uncertainty of returns). In addition, the level of Norwegian fishing effort off the west coast of Ireland over the period of decline in the Achill fishery would suggest that several thousand sharks were taken by them (McNally, 1976), perhaps being intercepted before reaching the confines of Keem Bay. Norwegian catches increased substantially around the time the Achill catch declined (Table I). As Myklevoll (1968) commented, "some of our (Norwegian) fishermen go as far as west and south of Ireland, much to the irritation of the Irish who sit on shore, waiting for shark to come to them". Add to this the discussion of cyclical periodicity in basking shark abundance and it becomes apparent that the views expressed by Parker & Stott (1965) greatly simplify the cause of decline in the Achill catch. The whole concept of highly localised discrete stocks can be called into question, and some consideration should be given to the hypothesis that the basking sharks at Achill are a small fraction of a greater seasonal invasion to waters to the west of Ireland, a feature which has always been evident according to McNally (1976).

Elasmobranch Population Dynamics

There have been several large scale fisheries specifically directed towards elasmobranchs, and exploitation has frequently occurred on a smaller scale enabling some properties of these fisheries to be determined. Some general conclusions can also be drawn from a consideration of the life-history characteristics of elasmobranchs.

Most elasmobranch species have low individual fecundities, producing a small number of eggs or young which exhibit a high rate of survival coupled to a slow relative growth rate and delayed age at maturity. On this basis Garrod & Horwood (1984) inferred that density dependent mechanisms for population regulation are likely to be weak and suggest that this will lead to a more direct relationship between the size of the mature stock and the number of young recruiting to the stock than in teleosts. Fishery management problems associated with the exploitation of elasmobranchs are discussed by Holden (1974, 1977). In particular he treats the determination of age, the estimation of growth and mortality rates, and the relevance of "classical" (teleost) population models and management strategies to non-teleost fisheries, concluding that none of the standard teleost assessment techniques are of immediate value when dealing with elasmobranch stocks. This is in part due to theoretical considerations but is also affected by the limited series of data available. Holden (1974, 1977) argued that by the time the young of elasmobranchs have reached a commercially exploitable size the number of female fish in the population is only sufficient to provide constant recruitment and sustained exploitation on mature females will directly reduce the size of the immature population as well as the mature stock. In answer to the question, "are sustainable fisheries for elasmobranchs possible?", Holden (1974) cited the history of several shark fisheries (Californian soupfin shark (Ripley, 1946), Australian school shark (Olsen, 1954), Scottish-Norwegian spiny dogfish (Holden, 1968) and Irish basking shark (Parker & Stott, 1965)) as evidence that after initial exploitation there follows at best a rapid decline in catch rates and at worst a total collapse of the fishery. Furthermore, in the era of large and very mobile fleets it is the nature of such fisheries that the point of rapid decline could be reached well before the necessary research has been carried out or the necessary data are available for management

policies to be enacted. Nevertheless, Holden argues that this does not rule out exploitation of elasmobranchs, but suggests that the scale of exploitation should be such that any decline in recruitment is small, remembering that the "surplus production" of elasmobranchs is not of the magnitude normally associated with teleosts.

Holden's accounts of the effects of exploitation on elasmobranchs may be unduly pessimistic in a number of the cases cited above. Although fisheries may have collapsed, the species concerned have never been threatened. Reports of a decline in the Australian school shark fishery were premature according to Kesteven (1966), who pointed to a substantial increase in the fishery from those levels which constituted a decline according to Olsen (1959), an increase which continued until 1972, when concern over elevated mercury levels in sharks led to the introduction of catch regulations (Grant, Sandland & Olsen, 1979). Hughes (1971) considered it likely that some of this increase is due to species other than school sharks. The decline in landings of the Californian soupfin shark recorded by Ripley (1946) confuses the true picture since 1940, when changes in landing practices introduced serious errors into the landings data (Roedel & Ripley, 1950). Although catches were much reduced (by 1950 the boom was over) soupfin sharks were abundant once more by 1956 (McCormick *et al.*, 1964).

Little is known for certain of the important biological parameters of basking sharks. Currently it is unlikely that any formal method of assessment based on catch data would be appropriate. Census data of the abundance of basking sharks in localised areas are limited in value as the number observed or estimated to be present at the time of the survey may reflect the erratic nature of the inshore invasions rather than changes in stock size or trends in abundance.

Current Status

That elasmobranchs are more vulnerable to exploitation than teleost fish species is widely recognised and concern is often voiced over the potential threat posed by commercial fisheries. For example, Brander (1981) said that demersal trawl and shrimp fisheries were involved in the disappearance of common skate (*Raia batis,* Linnaeus) from the Irish Sea. Cause for concern over basking shark fisheries is based on the decline in catch at Achill and the decrease in Norwegian landings over recent years (Table I), as well as the theoretical considerations discussed above. However, such an interpretation is likely to be too facile. The Achill decline may be due to the influence of Norwegian fishing effort and reduced Irish fishing effort as well as to changes in the sharks' behaviour, and the reduction in Norwegian landings can be attributed to market forces and the rationalisation of their fleet. Notwithstanding the fact that Holden (1974) may have been unduly pessimistic in his discussion of shark fishery collapses, he predicted only the likely collapse of elasmobranch fisheries, not threats to the existence of species.

Are basking sharks at present under threat? To view catch alone as a measure of abundance is to assume both constant effort by the fishermen and an unchanging catchability of their quarry, neither of which assumptions is justified in relation to the current basking shark fisheries. With respect to north-east Atlantic basking sharks Parker & Stott (1965), who attributed the decline at Achill solely to overfishing of a local stock, believed that the fishery presented no threat to numbers overall. Indeed, Stott (1974) asked UK fishermen the simple question "why ignore the basking shark?". More recently Gilbert & Gilbert (1986) wrote that "basking shark populations are so vast in many areas of both northern and southern hemispheres that the species is not considered endangered". Concern over local threats to the species may therefore be premature and misplaced.

Although the modern Scottish fishery is currently unregulated, catches are much smaller than those of the earlier post-war Scottish fisheries and are two orders of magnitude less than those which are assumed by some to have contributed to the collapse of the Achill Island fishery. The Norwegian fishery in waters around the British Isles has been very small since 1978, when EC-Norwegian agreements were first reached. There is no evidence that basking shark numbers are currently threatened. The Marine Laboratory, Aberdeen, is continuing to monitor the Scottish basking shark fishery and collate data from other nations, and welcomes the receipt of information from any source on stranded or incidentally caught basking sharks as well as information on any unusual appearances, either unseasonal or outside their normal domain.

Summary

The relatively sparse literature on basking sharks is briefly reviewed and aspects of their natural history are discussed along with the history of exploitation of this species. Basking sharks are distributed globally and are seasonal visitors to coastal waters in temperate and boreal latitudes. They are visible at the sea surface in calm, sunny conditions. The local distribution and numbers of basking sharks appearing annually off western European coasts are highly variable and it appears unlikely that they form locally discrete stocks. They are more likely to constitute larger, more diffuse populations. Little is known of many aspects of their life-history. They are ovoviviparous, producing six young in the only recorded instance of observed birth. No satisfactory method has been demonstrated for assessing the age of basking sharks and neither length nor age at maturity are known with any certainty.

Basking sharks are fished principally for their livers, although other products are also marketed. It is recognised that elasmobranchs are more susceptible than teleost fish to the effects of exploitation, yet, despite this, there is no firm evidence to suggest that the species has been threatened, even locally, by exploitation. The erratic nature of their seasonal appearances, coupled with marketing and economic difficulties, caused the failure of earlier UK fisheries and contributed to the decline of the post-war Irish fishery. A small scale UK fishery currently operates and the Norwegians continue to prosecute fisheries within EC waters as well as their own. These fisheries have recently been severely restricted owing to a collapse in the price paid for basking shark livers.

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